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## Sensitivity for reverse-phi motion

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### ABSTRACT

Low-level contrast information in the primary visual pathway is represented in two different channels. ON-center cells signal positive contrasts and OFF-center cells signal negative contrasts. In this study we address the question whether initial motion analysis is performed separately in these two channels, or also through combination of signals from ON and OFF cells. We quantitatively compared motion coherence detection for regular and for reverse-phi motion stimuli. In reverse-phi motion the contrast of a pattern flips during displacements. Sensitivity is therefore based on correlating positive and negative contrasts, whereas for regular motion it is based on correlating similar contrasts. We compared tuning curves for step size and temporal interval for stimuli in which motion information was limited to a single combination of step size and interval. Tuning for step size and temporal interval was highly similar for the two types of motion. Moreover, minimal coherence thresholds for both types of motion matched quantitatively, irrespective of dot density. We also measured sensitivity for so-called no-phi motion stimuli, in which the contrast of displaced dots was set to zero. Sensitivity for no-phi motion was low for stimuli containing only black or only white dots. When both dot polarities were present in the stimulus, sensitivity was absent. Thus, motion information based on separate contrasts was effectively cancelled by a component based on different contrasts. Together these results show equal efficiency in correlating dots of opposite contrast and of similar contrast, which strongly suggests efficient detection of correlations across ON and OFF channels.

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### 1. Introduction

Periodic reversals of the contrast of a moving pattern cause a reversal of perceived motion direction. (Anstis, 1970; Anstis & Mather, 1985; Anstis & Rogers, 1975). Classical explanations for this reversal have been based on the fact that contrast reversals simply shift the balance of motion energy to the opposite direction. The argument is easily illustrated with changes in space-time plots due to contrast reversals. Fig. 1A gives an example of rightward apparent motion of a random dot pattern of unlimited dot lifetime. In a space-time plot this type of motion shows up as an oriented pattern. In the space-time plot of Fig. 1B the same stimulus is combined with contrast reversals between displacements of the pattern. Obviously, the main orientation in the space-time plot has shifted 90 deg, indicating a reversal of motion direction, which is what observers report when presented with this motion stimulus. Fig. 1C and D show the Fourier transforms of these stimuli. In this representation the upper right and lower left quadrant represent motion energy for rightward motion, and the other quadrants for leftward motion. Evidently, reversing the contrast of

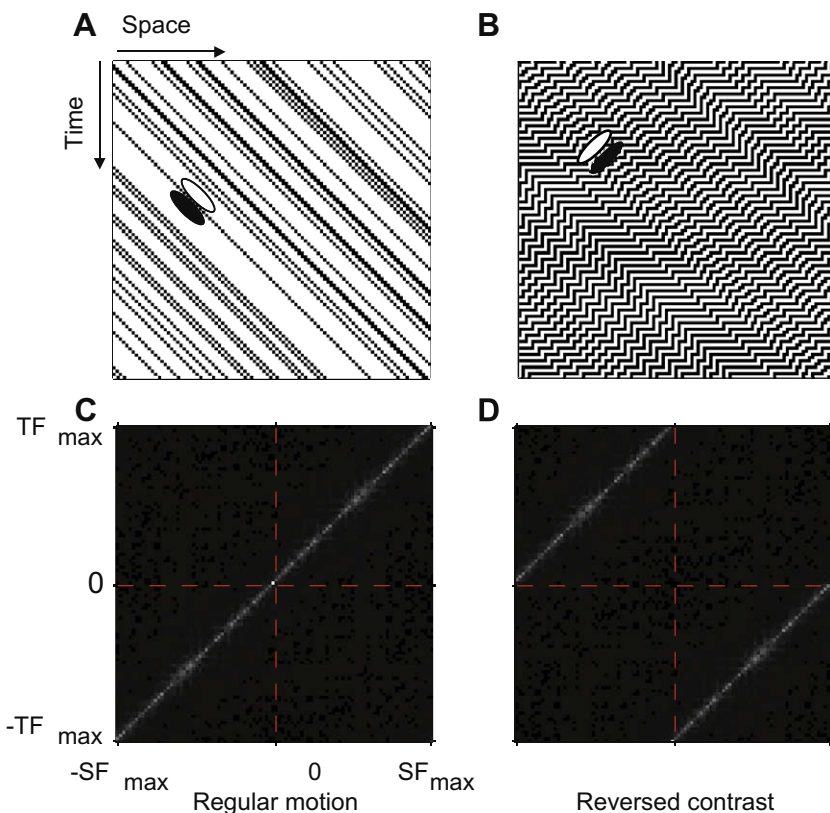
the pattern at successive frames results in a shift of motion energy to the complementary quadrants.

However, these representations of the stimulus do not explain how detection of these two types of motion comes about, and the low-level mechanisms responsible for detecting reverse-phi motion have remained controversial. In one view, the reversal is trivial because it is embedded in the stimulus and therefore requires no specific mechanisms. The argument is that any suitable motion detector would indicate the reversal of direction (Adelson & Bergen, 1985; Kregelberg & Albright, 2005; van Santen & Sperling, 1985). The idea is illustrated by the receptive field profiles of presumed motion energy detectors for rightward and leftward motion (Fig. 1). Obviously, the detector for rightward motion better matches the regular motion stimulus, whereas the leftward detector better matches the reverse-phi stimulus.

It should be noted though that Fourier transforms do not take into account that right from the retina contrast information is represented in two different channels. ON-center cells signal positive contrasts whereas OFF-center cells signal negative contrast. The two channels diverge at the level of retinal bipolar cells, and remain functionally segregated until convergence in primary visual cortex (Schiller, 1982, 1992; Schiller, Sandell, & Maunsell, 1986). Each channel provides a half-wave rectified representation of the visual image. In reverse-phi motion stimuli spatio-temporal correlations occur for dots of opposite-contrast polarity, that are

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**Fig. 1.** Regular and reverse-phi motion of a random pattern of unlimited dot lifetime. (A and B) Space-time plots for a coherently moving pattern in the rightward direction. Contrast reversals (B) on successive frames, i.e. along the time-axis, change the main orientation. Panels C and D show Fourier energy transforms of the space-time plots. The origin of the spatio-temporal frequency coordinates is centered in the panel. The oriented receptive field profiles shown in (A) and (B) correspond to presumed motion energy detectors for rightward (A) and leftward (B) motion.

presumably most effectively represented in different channels. In regular motion stimuli correlations occur for dots of similar contrast. Despite the description in terms of Fourier components one can therefore ask the question whether and how information from ON and OFF cells gets combined to generate motion sensitivity. Mo and Koch (2003) studied physiologically realistic models of low-level motion detectors, and argued that sensitivity for reverse-phi cannot easily be explained without specifically combining signals from ON- and OFF-center cells. Instead, they proposed that signals from the different cell types get combined at the first level of motion detection. In their model, motion information based on correlations between two ON or two OFF cells for one motion direction is always complemented by similar correlations between ON and OFF cells in the opposite direction.

In this study we tested a simple prediction from the hypothesis by Mo and Koch, i.e. that motion detectors combine signals from ON and OFF cells. Because motion detectors are hypothesized to combine opposite-contrast correlations as well as same-contrast correlations, the hypothesis predicts equal sensitivity for regular motion and for reverse-phi motion. Moreover, it predicts that spatio-temporal tuning for these different types of motion should also be comparable. If on the other hand reverse-phi sensitivity would somehow be based on responses within separate channels we would expect lower sensitivity for reverse-phi motion than for regular motion. In this case sensitivity for reverse-phi motion would result from correlating incremental responses for one contrast polarity, and decremental responses for the opposite-contrast polarity. These types of responses, e.g. an ON cell excited by a white dot and inhibited by a black dot, differ both in amplitude and in time course (Chichilnisky & Kalmar, 2002, 2003), resulting in relatively weaker correlations.

To critically test whether motion detection is based on balanced input from both ON and OFF cells, we compared sensitivity as a function of step size and temporal interval for regular and reverse-phi motion. Several previous studies partly addressed this problem. Edwards and Badcock (1994) reported that no motion was perceived in contrast-inverted random dot patterns, and concluded that information in ON and OFF channels remains segregated. Wehrhahn and Rapf (1992) similarly claimed that ON and OFF pathways form separate neuronal substrates for motion perception. Sato (1989), on the other hand showed that displacement limits for regular and reverse-phi motion were very similar. Most recently, Wehrhahn (2006) compared spatial and temporal limits using a two-flash apparent motion paradigm, and to quantitatively compare sensitivity to regular and reverse-phi motion. To this end, we constructed continuous versions of regular and reverse-phi motion stimuli that were highly similar except for the type of correlation. Rather than patterns with an unlimited dot lifetime as shown in Fig. 1 we used two-frame (single step) dot lifetime stimuli. Regular motion stimuli contained a correlation bias for same-contrast polarities, in which correlations for opposite-contrast polarities were fully randomized. Similarly, reverse-phi motion stimuli contained a bias in correlations between opposite contrasts, with randomized correlations for similar contrasts. Variations in step size

or temporal interval did not affect the spatio-temporal density of motion information, nor the duration or size of a stimulus. In combination with a variation of coherence levels these stimuli therefore allowed for a fair and quantitative comparison of tuning properties.

We found nearly equal sensitivity for regular and reverse-phi motion, and comparable step size and temporal interval tuning. Our findings therefore suggest that motion detectors effectively combine information within and across ON and OFF channels.

## 2. Methods

### 2.1. Stimuli

Visual stimuli consisted of sparse random dot patterns in which consistent motion information was either restricted to equal polarity correlations (regular motion) or to opposite polarity correlations (reverse-phi motion). Stimuli consisted of 5000 dots ( $0.02 \times 0.02$ ), presented in a window of  $8 \times 8$  on a gray background of  $50 \text{ cd/m}^2$ . Half of the dots were brighter and half were darker than the mean background (contrast 96%).

Motion information was confined to a single combination of step size and temporal interval. To this end we used single-step dot lifetime stimuli similar to those described in a previous study (Bours, Stuur, & Lankheet, 2006). A new set of random dots was generated and shown on each monitor frame (at 120 Hz), and these dots were shown once again at a displaced location after a specified temporal interval. New and displaced dots were shown transparently. Fig. 2 illustrates this type of motion. It shows a blow-up of a space-time diagram for a  $20 \times 20$  pixel matrix with black and white dots on a gray background. Dots are displaced once, with a step size of two pixels and temporal interval of two frames, and then randomly refreshed. Notice that, for temporal intervals longer than one frame the two instances of a dot are separated by frames in which newly generated dots are shown as well as displaced counterparts of previously generated dots. Interleaving correlated dots with uncorrelated dots clearly does not prevent motion detection: motion is easily perceived for temporal intervals up to at least eight frames (66 ms).

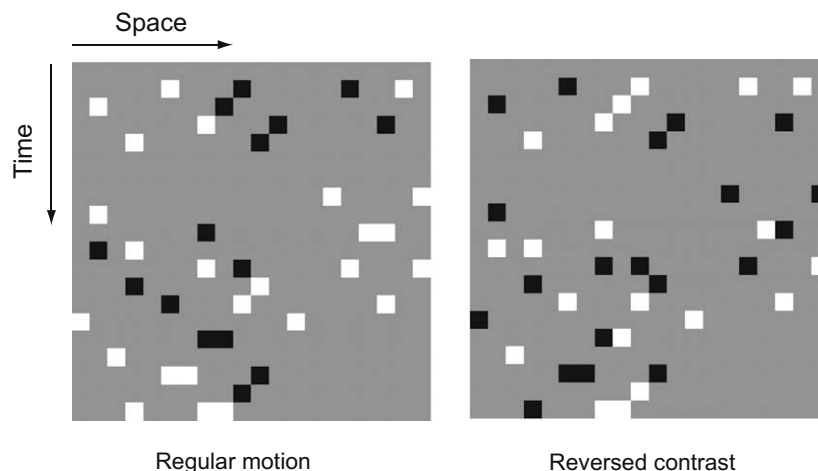
Each frame contained a combination of newly generated random dots and coherently displaced dots. This generates the same motion information on every frame of the monitor, and limits consistent correlations to the specified displacement and interval,

whereas all other combinations are fully randomized. Correlations over multiple steps in the apparent motion direction, which are abundant in unlimited lifetime stimuli, are completely randomized across motion directions. In contrast to other forms of continuous reverse-phi motion stimuli, our reverse-phi stimuli therefore contained no regular motion information at multiple time steps. Also, because dots were not visible during their temporal displacement interval, no net correlation existed for intervals shorter than the specified temporal interval. Because dots were refreshed on each frame of the monitor, irrespective of the temporal interval for displacements, variations in temporal interval did not affect the temporal frequency content of the stimulus. Changes in motion sensitivity with increasing temporal interval were, therefore, not confounded with changes in temporal frequency content or changes in temporal integration. Because each frame contained equal amounts of bright and dark dots varying the motion parameters or type of motion did not affect the temporal frequency content of the stimulus.

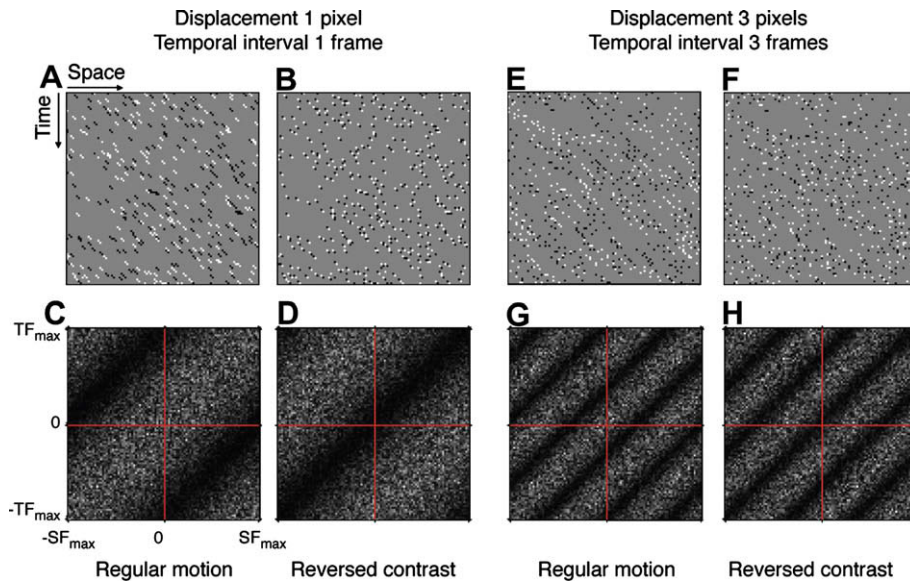
For regular motion, the two instances of a dot had the same polarity whereas for reverse-phi the polarity of dots was reversed upon displacement. Regular motion stimuli, therefore, contained no consistent correlations for combinations of opposite polarity, and for reverse-phi no correlations were introduced for dots of equal polarity. Notice, however, that introducing a correlation bias for same-contrast polarities induces a small imbalance for opposite-contrast polarities because presence of a same-contrast correlation automatically implies absence of an opposite-contrast correlation. In a control experiment we will investigate the relevance of this imbalance.

To measure sensitivity we varied motion coherence levels by changing the percentage of dots moving coherently. Incoherent dots were given a new random position upon displacements. At 100% coherence all reincarnated dots, i.e. half of all dots, were coherently displaced. By varying coherence levels rather than contrast, motion strength was manipulated without changing non-directional (local) contrast signals at levels before motion detection.

Fig. 3 illustrates the two types of motion. Fig. 3A–D illustrates motion of 1 pixel/1 frame and Fig. 3E–H show the example of 3 pixels/3 frames. Both examples correspond to the same speed at maximum coherence level. Space-time plots reveal the noisy character of the stimuli, due to the limited dot lifetime. For regular motion, orientation is easily discerned in the space-time plots. For



**Fig. 2.** Space-time plot of a continuous, single-step dot lifetime motion stimulus. The diagram shows a row of 20 pixels at 20 consecutive frames. Stimuli consisted of sparse random dot patterns with 50% black and 50% white dots on a gray background. Dots were shown only twice: the first time when they are newly generated, and a second time at a displaced location after a specified temporal interval. In this example dots were displaced two pixels rightward after two frames. New dots were generated on each frame of the monitor. For regular motion the corresponding dots have the same-contrast polarity, for reversed contrast a dot pair consists of a black and a white dot.



**Fig. 3.** Two-frame, single-step dot lifetime motion. (A and B) Space-time plots for regular and reverse-phi variants of the stimulus. (C and D) The corresponding Fourier energy plots. The origin of the spatio-temporal frequency coordinates is centered in the panel, as indicated by the red lines. (E–H) The same plots for different motion parameters. (A–D) 1 pixel/1 frame; (E–H) 3 pixels/3 frames. Dot densities are comparable to those in the actual stimuli, but for clarity only a quarter (100 pixels) of the actual width of the display is shown.

reverse-phi stimuli hardly any consistent orientation is perceived, yet observers could easily indicate the direction of motion in this type of stimulus. Fig. 3C and D shows the Fourier transforms of the space-time plots. In both cases the Fourier transform reveals a pattern of similar orientation. For regular motion this is a sinusoidal grating pattern with maxima on a line through the origin. For reverse-phi motion the pattern is shifted by 180 deg, with minima on a line through the origin. For a displacement of 1 pixel per frame the spatial and temporal transforms contain a single period of a sine wave. For larger displacements the number of periods grows correspondingly. In these stimuli the total motion energy for leftward and rightward motion is nicely balanced.

## 2.2. Measurement procedure

We used a left–right motion direction discrimination task in a two-alternative forced-choice procedure. Coherence thresholds were determined using a Quest adaptive staircase (Watson & Pelli, 1983), converging at 85% correct performance. For regular motion a correct response corresponded to the direction of displacement, whereas for reverse-phi ‘correct’ responses corresponded to the opposite direction. Staircases consisted of 40 trials of 1 s duration, in which the direction of displacements was randomly chosen to the left or to the right. Observers started a trial by pressing a key on the keyboard and responded by pressing the left or right arrow key. No feedback was given on the correctness of responses. Mean threshold values and standard errors were based on 3–5 repetitions for each condition, and all conditions were presented in randomized order.

## 3. Results

### 3.1. Regular and reverse-phi motion

Temporal and spatial tuning curves were measured for two naive observers and for the three authors. Fig. 4 shows results for two individual observers, and the mean for all five subjects. Temporal tuning curves were measured for a step size near the optimum for all observers (5 pixels, 0.1 deg, Bours et al., 2006). Step size tun-

ing curves were measured at three temporal intervals (1, 3 and 8 frames; 8.3, 25 and 67 ms). We found that, for the full range of step sizes and temporal intervals, thresholds for both types of motion were highly similar. Highest sensitivities, corresponding to the lowest coherence thresholds, matched and occurred at the same combination of step size and temporal interval. There was a significant tendency for lower sensitivity for reverse-phi at large temporal intervals and large step sizes, but on average this effect was relatively small. In the discussion we will come back to these differences.

The optimal temporal interval was about 25 ms (3 frames) both for regular and for reverse-phi motion. At the lower end, sensitivity dropped fairly steeply, but the maximal frame rate of 120 Hz in our setup did not allow us to determine the lower temporal limit. The upper temporal interval limit was between 75 and 100 ms. Notice that this upper limit was measured with dynamic noise in between the first and second presentation of a dot, and therefore provides a lower bound to the upper limit. Still, this value is much higher than the limit reported by Wehrhahn (2006).

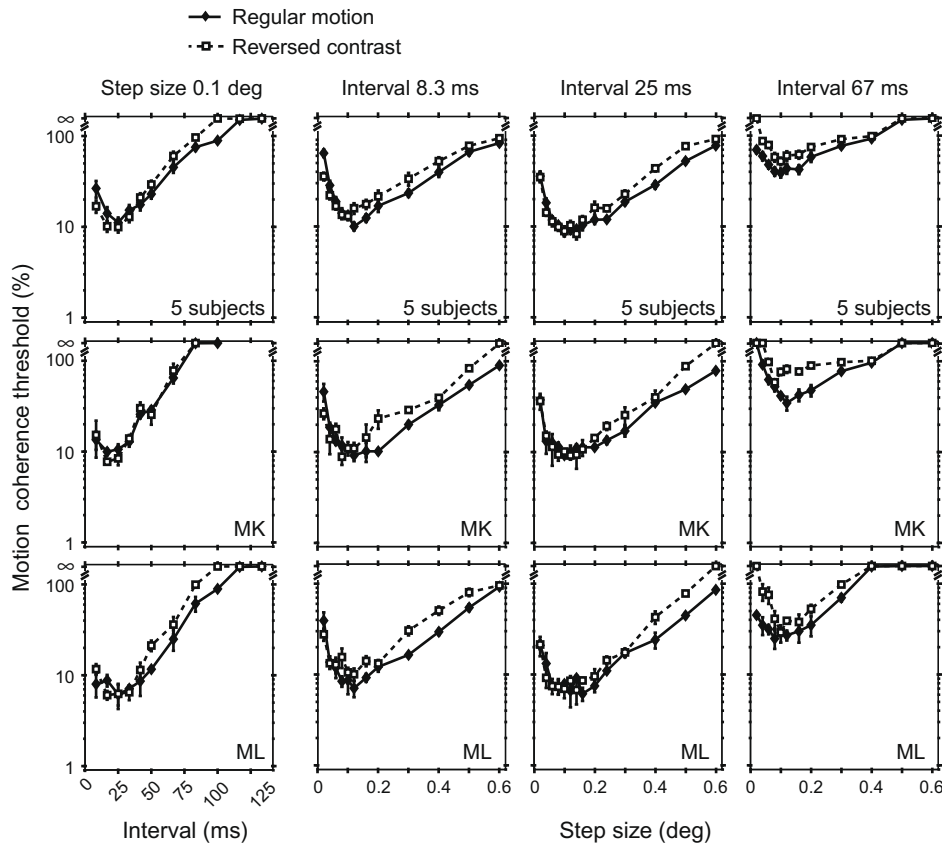
Optimal step sizes for both types of motion were about 7 min of arc. Upper displacement limits were about 36 min of arc, which is also higher than reported by Wehrhahn. Our data show a gradual decline of sensitivity for both types of motion, indicating that there is no obvious reason to propose a qualitatively different mechanism for detecting these large step sizes.

The high similarity in sensitivity and tuning properties for regular motion and reverse-phi motion indicates that motion mechanisms combine positive and negative contrasts as efficiently as similar contrasts. This strongly suggests equality of the low-level contrast responses being used in both cases, which is only possible if correlation for reversed-contrast stimuli occurs across different channels.

### 3.2. No-phi motion

An alternative explanation for the reversal of motion direction when the contrast is periodically inverted might be that no specific correlation is required at all. In this view, flipping the contrast removes positive correlations at the specified combination of step





**Fig. 4.** Temporal and spatial tuning for regular and reverse-phi motion. Left–right discrimination thresholds were determined by varying the percentage of dots moving coherently, in a staircase tracking the 85% performance level. Each condition was repeated three times. Data are shown for two individual observers (error bars: SEM,  $n = 3$ ), and the average for five observers (error bars: SEM,  $n = 5$ ). Temporal tuning curves were measured using a step size of 0.1 deg (5 pixels) and step size tuning curves at three different temporal intervals.

size and temporal interval, and therefore makes the opposite displacement relatively more frequent. For example, if rightward displacements of a dot were consistently absent because the contrast inverts, displacements in the leftward direction would be relatively more frequent, due to random noise. Because motion is opponently organized, such a reduction in same-contrast correlations might tip the balance towards the opposite direction and hence induce a reversal of perceived direction. If removing same-contrast correlations were the main point, this could also explain the similarity in tuning properties for regular and reverse-phi motion, because exactly the same motion detectors would be involved.

We investigated this hypothesis by creating a stimulus in which the second instance of a dot (i.e. the displaced reincarnation of a previously shown dot) was drawn in the background luminance. Notice that this is different from not drawing the dots at all. Drawing in the background color removes any dots drawn at that location and thus removes specific correlations, without introducing opposite-contrast correlations. One could call this a no-phi stimulus: the contrast is neither the same nor inverted. Such a no-phi stimulus removes specific same-contrast correlations in the same way as a reverse-phi stimulus does, but does not introduce opposite-contrast correlations.

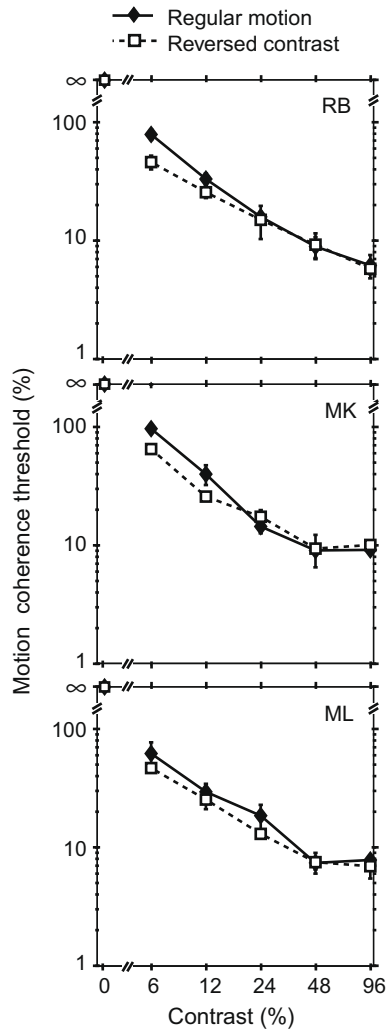
In a control experiment we measured the effect of decreasing the contrast of displaced dots, from the maximum value of 96% down to the no-phi condition of 0% contrast. We measured sensitivity for regular and for reverse-phi motion for an optimal combination of step size (5 pixels, 0.1 deg) and temporal interval (3 frames, 25 ms). The contrast of the second instance of a dot was reduced from 96% to 0%, while the contrast of the first occurrence of a dot was held

constant at 96%. All other parameters were identical to those in the previous experiments. If removal of correlations from the stimulus caused direction reversals in reverse-phi stimuli, we would expect observers to be quite sensitive to no-phi motion, and results to be independent of the contrast of the second dot.

Results for this control experiment were very clear: at zero contrast none of the observers could consistently indicate the direction of this type of no-phi motion. Everyone performed at chance level, even at the maximum coherence value. Fig. 5 shows results for different contrasts of displaced dots. Reducing the contrast from 96% to 48% had little effect on motion coherence thresholds. Further reducing the contrast, however, progressively deteriorated motion coherence detection. At zero contrast (the no-phi condition) motion was observed neither in the direction of displacement nor in the opposite direction.

We conclude that lack of correlations does not play a large role in explaining sensitivity to reverse-phi motion. If it was a significant contribution the effect of contrast for the reversed-contrast stimuli should have been very small, and the contrast curve should have been flat. Instead, we see that sensitivity falls only slightly less steeply for reversed-contrast motion than for regular motion. Clearly, it is not just the absence of a consistent correlation that matters, but also the quantitative contrast mismatch between corresponding dots.

The results in Fig. 5 were obtained for stimuli containing both black and white dots, similar to the stimuli in the first experiment. We were surprised to find a complete lack of motion sensitivity for the no-phi stimulus, because it clearly contains motion information. For both black and white dots there is an imbalance in spa-



**Fig. 5.** Coherence thresholds as a function of contrast. The contrast of the second appearance of a dot was varied, while keeping the contrast of the first appearance at a fixed (maximum) level. At zero contrast the second appearance is drawn in the background luminance. Notice that this is different from not drawing the dots at all. Drawing in the background specifically removes correlations, and thus induces a directional imbalance. Random dot patterns consisted of black and white dots on a mean background. An infinite threshold indicates that performance did not reach the required 85% correct level. Error bars represent SEMs ( $n = 3$ ).

tio-temporal correlations. In order to further study why no motion was observed in the no-phi condition we repeated the experiment for stimuli that contained different combinations of black, white and background dots. Results are shown in Fig. 6. The first condition corresponds to the regular motion stimulus in which half of the dots were black and half were white. Conditions two and three are regular motion stimuli in which all dots are of similar contrast. Conditions 4–6 are the reverse-phi versions of the same stimuli. The last three conditions are three versions of a no-phi stimulus; with only white dots, only black dots, or a combination of black and white dots (i.e. the zero contrast condition from the contrast experiment). Notice that dot densities and mean luminance levels may be different for the different conditions, but they did not change during stimulus presentations, and did not affect the results significantly.

Highest sensitivities, i.e. lowest coherence thresholds were obtained for stimuli in which the first and second instances of dots were either black or white. It did not matter very much whether they were black, white or flipped contrast. In all cases observers

reached coherence thresholds of about 5–10%. For the no-phi stimuli containing only black or only white dots observers performed well above chance and reported motion in the direction opposite to the displacements. Thresholds were however between 70% and 90%, much higher than for standard reverse-phi motion. For the no-phi stimulus containing both black and white dots, i.e. the stimulus used in Fig. 5, observers performed at chance level, as indicated by an infinite threshold. These data show that lack of correlations may indeed cause a directional imbalance, which can be perceived as coherent motion. However, this effect is far too weak to explain sensitivity to reverse-phi motion. Moreover, the effect completely disappears if black and white dots are combined in a single motion stimulus.

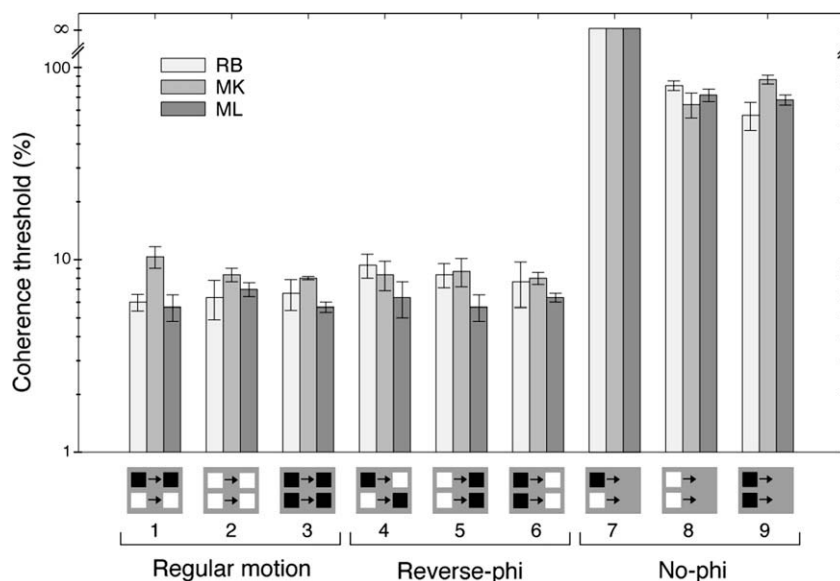
In fact, the absence of motion sensitivity for mixed-contrast no-phi stimuli adds further support for the claim that motion detectors combine same-contrast polarities and opposite-contrast polarities with similar efficiency. If motion analysis would have been limited to similar contrasts, without cross talk between the two channels, it is difficult to explain why the motion percept vanished if black and white dots were combined in a stimulus. Absence of correlations would signal a similar motion direction for disappearing black and white dots. However, observers do not see this type of motion, presumably because the component based on separate contrasts is cancelled by a component based on correlations between black and white dots (corresponding to motion in the opposite direction). Cancellation of motion signals in a no-phi stimulus therefore suggests that opposite polarity correlations perfectly counteract the directional imbalance created for each polarity separately.

### 3.3. Dot density

Our results agree with combining information from ON and OFF channels into low-level motion detectors. So far, however, we did not rule out that information from positive contrasts and negative contrasts gets combined at a level before motion detection. The extent to which this might occur depends largely on the degree of low-level spatio-temporal integration of luminance information. If receptive fields of ON and OFF cells extensively integrate positive and negative contrasts, each dot polarity will have a similar but opposite effect. In this case, both dot polarities would have nearly equal efficiency in modulating responses of both ON and OFF cells. Thus, equal efficiencies for regular and reverse-phi motion might have resulted from convergence and integration of opposite polarity responses in ON and OFF channels, i.e. prior to motion detection.

To examine the contribution of low-level luminance integration we compared sensitivity for regular and reverse-phi motion as a function of dot density. Reducing dot density effectively reduces the effects of spatio-temporal luminance integration in ON and OFF cells. As a result responses in each cell type will be more dominated by their preferred contrast polarity. Reducing dot density should therefore reveal any asymmetries. More specifically, if low-level luminance integration would play a major role, reducing dot density should cause a much larger reduction in sensitivity to reverse-phi motion than to regular motion.

Fig. 7 shows the results for variation of dot density. We measured sensitivity at the optimal combination of step size (0.1 deg, 5 pixels) and temporal interval (25 ms, 3 frames) for dot densities varying from 2.5 to 320 dots/deg<sup>2</sup>. Our data show no consistent signs of sensitivities diverging at lower dot densities. Observer MK shows lower thresholds for reverse-phi motion at low dot densities, which is opposite to what we would expect based on low-level luminance integration. This result makes it unlikely that positive and negative contrasts are represented equally efficient in both ON and OFF channels.



**Fig. 6.** Motion coherence thresholds for regular, reverse-phi and for no-phi motion. Dots were either black or white at maximum contrast, or drawn in the background color (zero contrast). The cartoons below each column indicate the contrast of the first (left) and second (right) appearance of a dot. Zero contrast is indicated as the absence of a square. For each condition the upper and lower squares in the cartoon represent the contrasts of half of the dots. Coherence thresholds below 100% indicate performance above chance level (at least 85% correct). For the no-phi conditions with both black and white dots observers performed at chance level. Error bars show SEMs ( $n = 3$ ).

#### 4. Discussion

The motion stimuli that we used in the present study have several advantages over those used previously. First, motion information is limited to a specific combination of step size and temporal interval, which allows for accurate and specific measurements of motion tuning properties (see also Bours et al., 2006). Second, the stimuli allowed us to create regular motion in which no correlation bias between opposite contrasts was present, and reverse-phi motion in which no bias was present for similar-contrast correlation. For regular motion correlations between opposite contrasts were completely randomized, and for reverse-phi correlations between similar contrasts were randomized. Sensitivity and tuning for the two types of motion could therefore be compared quantitatively. Third, by using motion coherence to compare sensitivities we specifically addressed motion detection, without affecting local, low-level luminance or contrast information. Moreover, variations in motion parameters did not affect the time course of motion information: each frame contained statistically the same amount of motion information, irrespective of temporal interval. This is different from classical two-flash stimuli, in which motion information is generated at intervals corresponding to the temporal interval of displacements. Therefore, variations of inter stimulus interval always affected temporal integration of motion signals as well. In our experiments, motion information was generated on each frame of the monitor, and temporal integration of motion signals was not affected by changes in temporal interval.

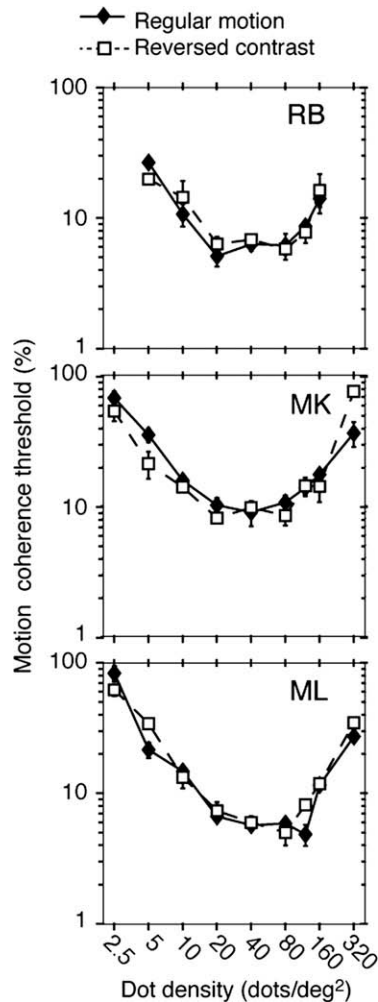
Our results showed that sensitivity and tuning properties were very similar for regular and for reverse-phi motion. This observation extends the finding by Sato (1989) and Wehrhahn (2006) that displacement limits are similar for regular and reverse-phi motion. In addition to the similarity in spatial and temporal limits, our data show that absolute levels of sensitivity are nearly the same, and also the combination of step size and temporal interval at which they occur.

Our conclusion is that low-level motion detectors are equally efficient in combining same polarity signals and opposite polarity signals. Similar sensitivity to regular and reverse-phi motion makes it highly unlikely that reverse-phi sensitivity is based on

correlation within separate ON and OFF channels. For high-contrast stimuli, such as the ones we used, ON and OFF responses in a single channel are very different (Chichilnisky & Kalmar, 2002). For example, the response of an ON cell to a bright dot consists of an increase in spike frequency. The response of the same cell type to a dark dot would be a reduction in spike frequency. These two types of responses differ considerably in amplitude as well as dynamics, especially at high contrast levels (Chichilnisky & Kalmar, 2002) and low dot densities. As a result our subjects should show a large difference in sensitivity if their detection of regular and reverse-phi opponent-motion were based on correlations within the same channel. We found similar sensitivities down to the lowest dot densities, and at all contrast levels. We therefore conclude that motion detection is most likely based on similar low-level responses from both ON and OFF cells, i.e. on positive contrasts exciting ON cells and negative contrasts exciting OFF cells.

Findings for the no-phi stimuli support this argument. Observers perceived motion in the so-called no-phi stimuli, but only if the stimuli contained a single contrast polarity. However, sensitivities were very low compared to the regular and reverse-phi motion stimuli. If both black and white dots were present no motion was perceived at all. This implies correlation of opposite polarities that is as efficient as correlation of similar polarities. These opposite-contrast combinations generate 'reverse-phi' motion percepts in the direction opposite to those for same-contrast combinations. The fact that the motion percept was totally absent suggests that the two motion signals were equally strong, and cancelled each other.

Our findings are at odds with many previous reports arguing against combination of ON and OFF channels in low-level motion detection (e.g. Edwards & Badcock, 1994; Mather, Moulden, & O'Halloran, 1991; Wehrhahn & Rapf, 1992). Edwards and Badcock, for example, found no sensitivity to contrast-reversed motion in moving random dot patterns and concluded that ON and OFF channels remain segregated at the level of local motion detection. Our results, however, show that motion detection is in fact equally efficient with and without contrast reversals. Various different findings in previous experiments are likely due to differences in motion stimuli. We specifically constructed our stimuli to allow



**Fig. 7.** Sensitivity for regular and reverse-phi motion as a function of dot density. Thresholds were measured in a staircase procedure tracking the 85% correct performance level. Step size and temporal interval were fixed at optimal values (0.1 deg, 25 ms). Error bars show SEMs ( $n = 3$ ).

for a direct comparison of tuning properties and minimal confounds of variations in luminance integration and changes in higher-level motion integration due to changes in stimulus duration and time course of motion information. An important difference between our stimuli and those used in previous studies may be due to different contributions from second order motion mechanisms. A second order motion mechanism that discards the sign of luminance contrast (Chubb & Sperling, 1988) will respond in similar ways to regular and to reverse-phi motion. Notice that for reverse-phi stimuli the effects of first order motion and second order motion are therefore opposite, and will cancel one another. For regular motion however, the two mechanisms yield similar signals and will add up. A small contribution from second order motion detectors could thus explain the relatively lower sensitivity for reverse-phi motion, especially because the second order system is favored by slow motion (Papathomas, Gorea, & Chubb, 1996) and large displacements (Sperling, 1989). For our continuous stimuli with high degrees of dynamic noise second order mechanisms presumably play only a minor role, whereas in more classic two-frame paradigms with recognizable patterns it may play a very significant role.

The notion that sensitivity to our reverse-phi stimuli is most likely based on combining signals from ON and OFF cells does not exclude that differences in response timing may also induce illusory motion percepts. Del Viva, Gori, and Burr (2006), for

example, recently showed that contrast-inverted Glass patterns, in which the paired dots are shown simultaneously, generate a clear motion percept. This was consistent with a small time delay in processing of positive contrasts relative to negative contrasts. The difference was on the order of a few milliseconds, which is well in line with the difference in dynamics between ON and OFF cells (Chichilnisky & Kalmar, 2002). If delay differences were compensated in the timing of bright and dark dots in the stimulus, the imbalance disappeared. This finding is not at odds with nearly similar tuning for our stimuli. Differences of a few milliseconds would cause only minor differences in temporal tuning curves because tuning for inter-displacement interval is fairly broad. The difference in response dynamics for ON and OFF cells might in fact be a second reason for the different sensitivities at large inter-displacement intervals. In this range, the interval is limiting, and an additional time delay between channels would affect sensitivity to reverse-phi motion, but not to regular motion.

Our data provide additional support for the combination of ON and OFF cell signals in generating low-level motion signals. These motion signals do not primarily result from small timing differences in responses from ON and OFF cells, but from equal treatment of correlations within and across channels. Theoretically this makes sense, because in this way, motion detectors optimally use all available information. For a coherently moving pattern motion information is not only contained in the presence of positive correlations within separate channels, but also in the absence of correlations across ON and OFF channels. In other words, correlations between different contrasts signal the absence of motion. Combining positive and negative evidence for one direction of motion at an early level is an efficient way to improve the signal to noise ratio. Our data support the hypothesis that motion detectors use both types of information. Reverse-phi motion is then simply explained as a side effect of the second type of motion information.

This notion is in line with the general assumption in motion energy models that motion energy extraction is based on full, non-rectified contrast signals. At the same time, similar sensitivity and tuning properties for reverse-phi and regular motion force one to consider how low-level contrast signals are used in motion detection. A description in terms of Fourier energy does not take into account the fact that contrast is represented in separate ON and OFF channels. Moreover, it is not trivial to explain sensitivity for our stimuli based on spatio-temporal frequency content. Global integration over different quadrants obviously does not suffice, since the total Fourier energy for leftward and for rightward motion is typically nicely balanced in our stimuli, both for regular and for reverse-phi stimuli. Fig. 3 shows that, especially for larger step sizes and temporal intervals complementary quadrants contain equal amounts of Fourier energy. The main difference between regular and reverse-phi motion is a phase shift of the pattern. In both cases, however the total energy for leftward and rightward motion is similar. Simple linear summation of energy for the two directions therefore cannot explain sensitivity for our stimuli. To explain our findings one has to assume more complex, nonlinear combinations of different Fourier components. This conclusion is in line with findings by Krelberg and Albright (2005). Based on single cell recordings in area MT of macaque monkeys they also concluded that linear combinations of motion energy components could not explain responses to more complex stimuli. Their data revealed complexities in the integration of motion components that are not normally incorporated in motion energy models.

Rather than specifying the complex integration of Fourier components, our experiments specifically addressed the way low-level contrast signals are used to generate directional selectivity. Our findings strongly support the notion by Mo and Koch that sensitivity for reverse-phi requires direct correlations between displaced ON and OFF cells.



Notice that the requirement for combining signals from ON and OFF cells does not specify exactly how such correlations cause a direction reversal. In a related paper we showed that reverse-phi percepts in many respects behave like motion aftereffects. This suggests that, similar to aftereffects, low-level responses to reverse-phi motion consist of low-level inhibitions. Rather than exciting detectors tuned for motion opposite to the direction of displacements, opposite-contrast correlations generate inhibitions for the direction of displacements (Bours, Kroes, & Lankheet, 2007). Because the motion system is opponently organized such a low-level inhibition translates into an excitation into the opposite direction at a higher level (Grunewald & Lankheet, 1996). We therefore propose that reverse-phi motion results from direct combinations of ON and OFF cell signals that cause inhibition at the detection level, and due to disinhibition cause excitations at higher levels, and motion percepts for opposite directions.

### Commercial relationships

None.

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